

A PROBABLE NEOTELEOST, DUGALDIA EMMILTA GEN. ET SP.
NOV., FROM THE LOWER CRETACEOUS OF QUEENSLAND,
AUSTRALIA

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A new teleost, *Dugaldia emmilta* gen. et sp. nov., from the marine Toolebuc Formation (Lower Cretaceous, Albian) of Queensland has a tripartite occipital condyle (exoccipitals and basioccipital) indicating affinities with the Neoteleostei; there is insufficient evidence to allow its referral to a particular order. A number of characters common throughout teleosts are present in *Dugaldia*: a berciform foramen in the anterior ceratohyal, numerous branchiostegal rays, fusion of the parietals, the presence of a supraorbital and large intercalars and the absence of a basiptyergoid process. This set of characters suggests that *Dugaldia emmilta* is a primitive neoteleost.

□ *Osteichthyes, Neoteleostei, Cretaceous, Australia*

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To date only four Cretaceous actinopterygians have been described from Queensland: *Cooyoo australis* (Woodward, 1894); *Pachyrhizodus marathonsensis* (Etheridge jr, 1905); *Flindersichthys denmeadi* Longman, 1932; and *Belonostomus sweeti* Etheridge jr & Woodward, 1892. *Pachyrhizodus marathonsensis* and *C. australis* were redescribed by Bartholomai (1969) and by Lees and Bartholomai (1987) respectively.

A fifth actinopterygian, *Dugaldia emmilta*, is represented by a single specimen (GSQ9242) which is sufficiently well-preserved to show details of the neurocranium, palatoquadrate, opercular bones, hyoid apparatus and pectoral girdle. The specimen was collected from Early Cretaceous (Albian) sediments of the marine Toolebuc Formation, in the Cloncurry district of northwestern Queensland, and was prepared by etching in dilute acetic acid (technique modified from Toombs & Rixon, 1953).

SYSTEMATIC PALAEOONTOLOGY

ACTINOPTERYGII

Subdivision: NEOTELEOSTEI

Order and Family uncertain

DUGALDIA gen. nov.

Type and only species *D. emmilta* sp. nov.

ETYMOLOGY

The specimen was collected from the Dugald River, Queensland.

Dugaldia emmilta gen. et sp. nov. (Figs 1-6)

HOLOTYPE
GSQ 9242

ETYMOLOGY

Emmiltos Greek — tinged with red, referring to the colour of the limestone from which the specimen was collected.

HORIZON AND LOCALITY

Dugald River, Granada Station, north of Cloncurry, NW Queensland, Lat. 20° 12'S, Long. 140° 55'E. Marine limestones of the Toolebuc Formation, Lower Cretaceous, Albian.

DIAGNOSIS

Frontals broad and flat, forming about three-quarters of the neurocranial roof. Each is laterally rugose, with ridges extending anteriorly and posteriorly from a centre of ossification at posterior half of the lateral margin. Large intercalars located at postero-ventral corners of occiput, articulating with lateral margins of exoccipitals and postero-ventral corners of pterotics. Antero-lateral corner of sphenotic extended into ventral spur, with antero-ventral surface of this bone defining part of hyomandibular fossa. Dermethmoid meets frontals in semicircular interdigitating suture. Anterior surface exhibits large, median ridge extending downward onto vomer. Laterally the dermethmoid

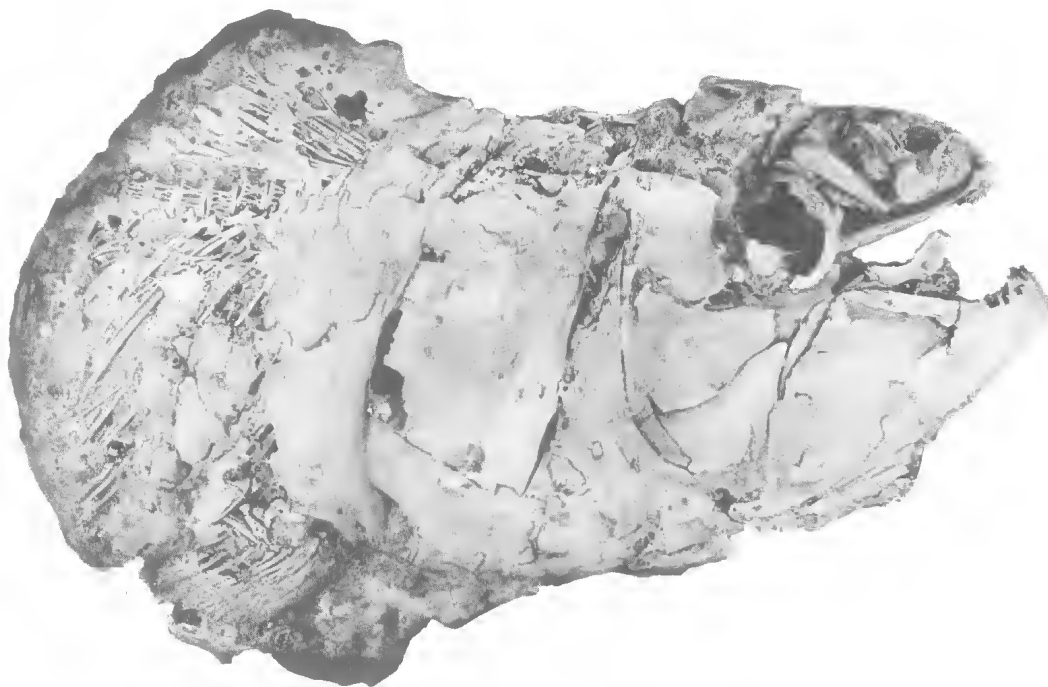


FIG. 1. *Dugaldia emmilla* gen. et sp. nov. Holotype (GSQ 9242), Albian Toolebuc Fm., Qld, right lateral view, showing external structure, approximately X 0.7.

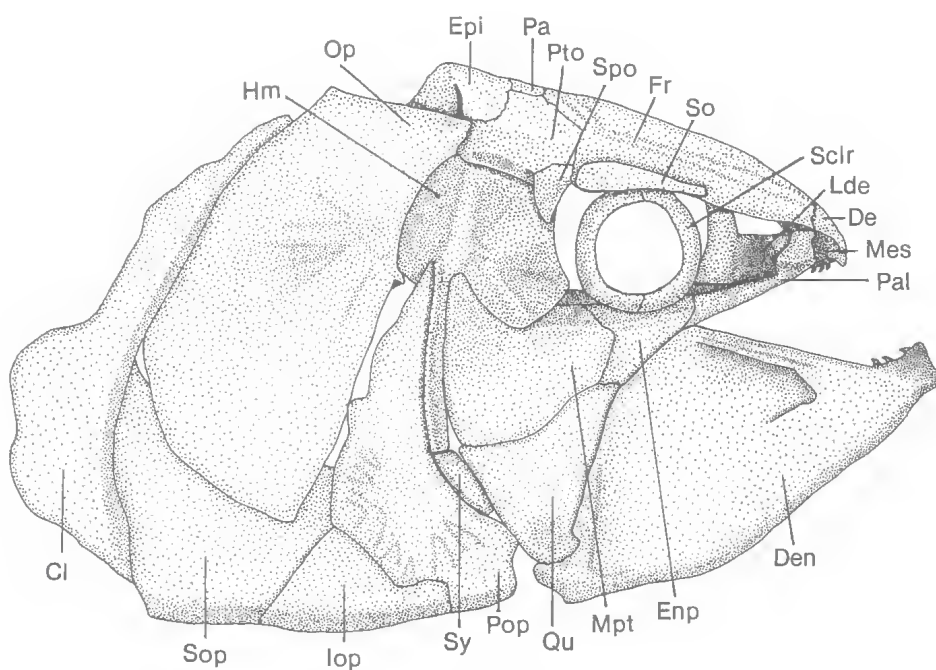


FIG. 2. *Dugaldia emmilla* gen. et sp. nov. drawn from GSQ 9242. Restoration in right lateral view showing external structure, approximately X 0.75.



FIG. 3. *Dugaldia emmilta* gen. et sp. nov. GSQ 9242, left lateral view showing internal structures, X 0.75

overlies the mesethmoid. Mesethmoids developed into prominent curved wings that combine with lateral dermethmoid to form a facet for head of the palatine. The lateral dermethmoid is large and rectangular, a dorso-ventral depression dividing its lateral surface in two. A strut extends upwards from postero-dorsal surface of mesethmoid to articulate with ventral surface of frontals. Upper and lower hypohyals are joined by an interdigitating suture.

DESCRIPTION

NEUROCRANIUM

Viewed from the side the neurocranium (Figs 4, 6) is wedge-shaped. Its ventral margin is formed by the parasphenoid and its roof by the frontal and ethmoid bones. The posterior margin of the neurocranium is formed by the occipital bones. Dorsally the neurocranium is almost rectangular in shape.

Most of the dorsal surface is formed by the large flat frontals, which meet along a midline suture (obscured by damage posteriorly). Anteriorly the frontals join the dermethmoid by means of a posteriorly-curved semicircular denticulate suture (Fig. 5). Postero-laterally they are flanked by anterior extensions of the pterotics and posteriorly they meet the parietals. Centrally, the frontals are flat and unornamented (Figs 4, 5); laterally, ridges extend to the anterior and posterior margins of the bones. These ridges radiate from centres of ossification at the lateral margins of the frontals, approximately two-thirds of the way back from the anterior margin. The posterior margins of the frontals converge to meet at a point on the midline of the neurocranium, forming a U-shaped tongue of bone. This margin of the frontals is very weathered, making it difficult to interpret exactly the relationships of the bones in this region, particularly the form of the parietals. Thus it is not possible to determine positively whether or not the parietals join along the midline or are separated by

the supraoccipital. However, the material that has been preserved indicates that the parietals were not separated by the supraoccipital but that they meet at the midline of the neurocranium. The parietals extend antero-laterally to enclose the V-shaped salient formed by the posterior parts of the frontals.

The pterotics (Figs 4, 5) are large bones, lying lateral to the parietals, which cover most of the postero-lateral surface of the neurocranium. They extend forwards to meet the frontals dorsally and the sphenotics ventrally, and they extend backwards to join the epiotics and exoccipital. The ventro-lateral surface of the pterotic forms the posterior half of the hyomandibular fossa, and the postero-ventral corner is extended into a pterotic spine. The lateral surface is vertically striated. On the antero-lateral corner is an elliptical depression which probably represents the lateral temporal fossa. This extends forwards onto the postero-ventral corner of the sphenotic.

The sphenotic (Fig. 4) forms the posterior margin of the orbit. Its antero-lateral corner is developed into a ventrally directed spur, while its postero-lateral corner defines the post-temporal fossa. Ventrally the sphenotic bears the anterior portion of the large hyomandibular fossa, which extends almost the entire length of the otic region of the neurocranium. It is a simple, horizontal, elongate depression of almost uniform width, though it is slightly expanded at its posterior and anterior ends. Ventro-medially the sphenotic meets the prootic.

The prootic (Fig. 4) is partly obscured by fractures and seems to have been pushed dorsally into the neurocranium. It appears to be a robust bone which articulates posteriorly with the basioccipital and the exoccipital, and ventrally with the parasphenoid. It shares an interdigitating suture with the ascending process of the parasphenoid.

The large exoccipitals (Figs 4, 6) cover most of the ventral half of the occiput. They form the dorsal

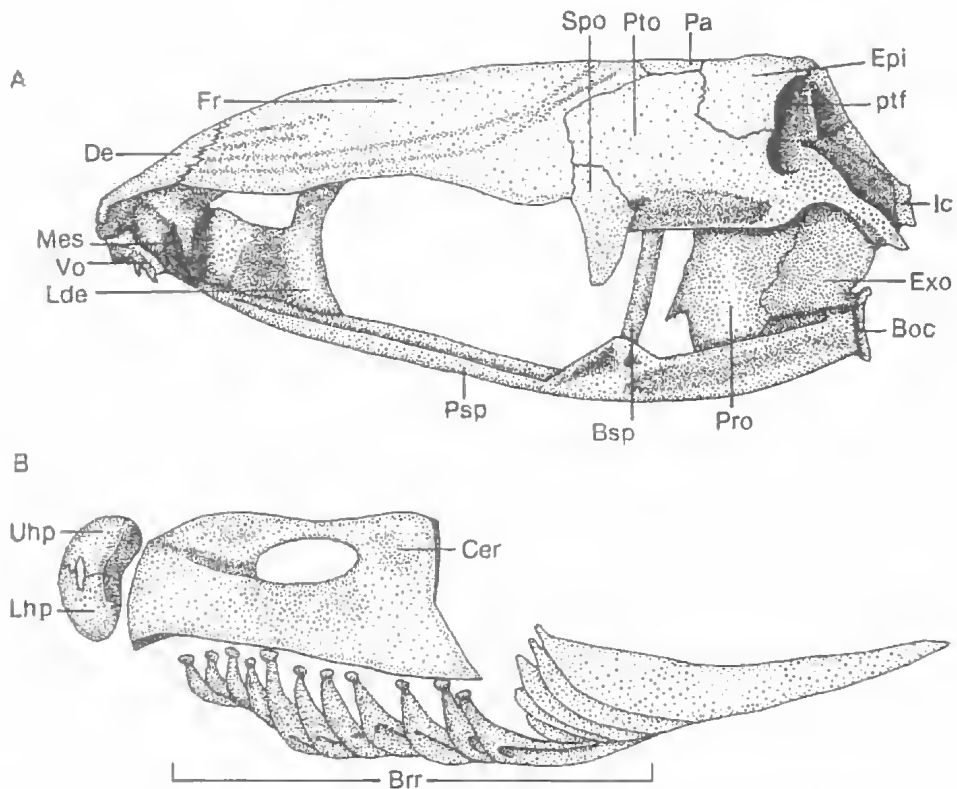


FIG. 4. *Dulgalidia emmilla* gen. et sp. nov. drawn from GSQ 9242, A. Neurocranium, left lateral view, X 1.35, B. Branchiostegal support and rays, left lateral view, X 1.1.

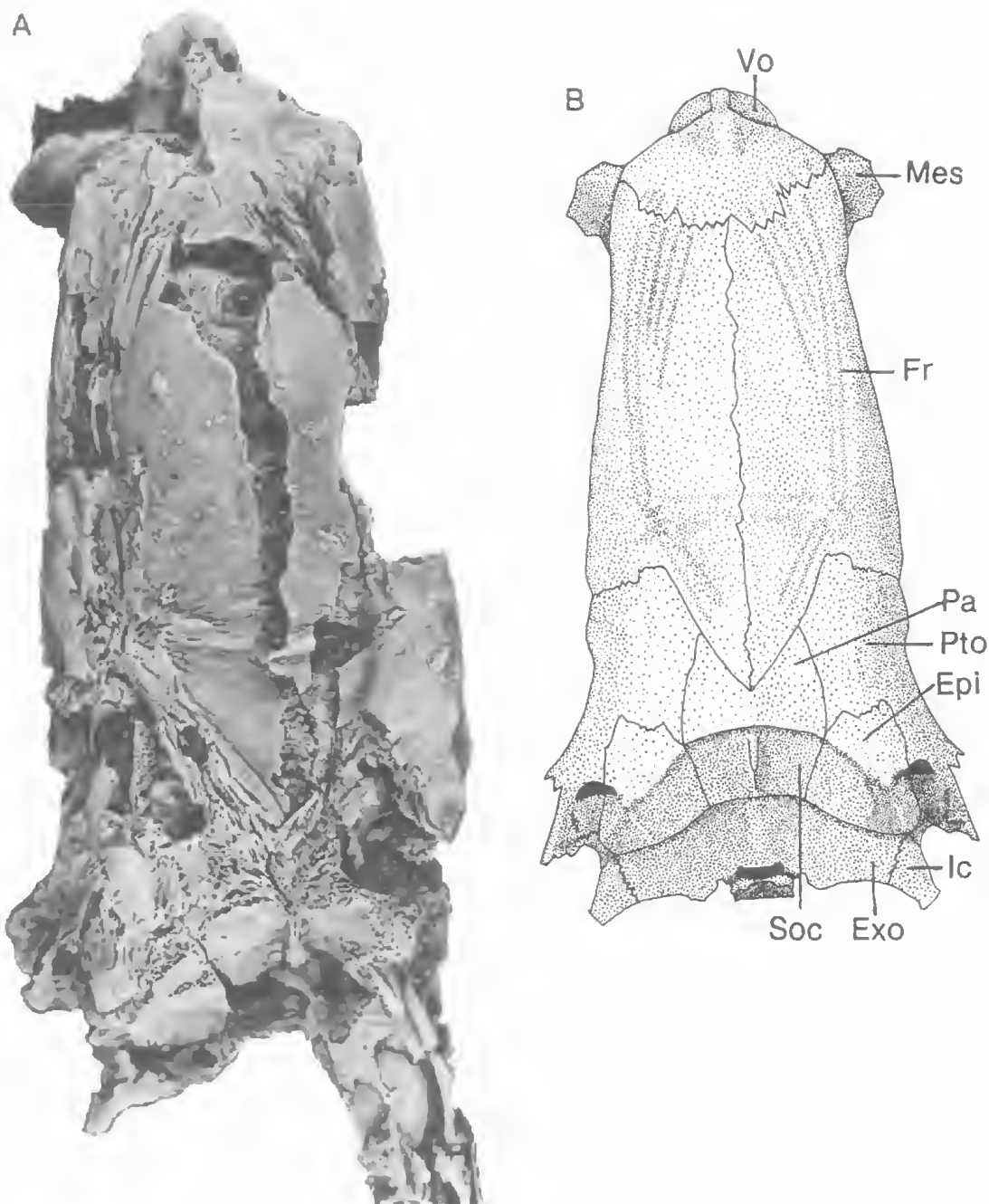


FIG. 5. *Dugaldia emmilta* gen. et sp. nov. A. Holotype (GSQ 9242) Dorsal view of neurocranium, X 1.7. B. Restoration of neurocranium in dorsal view, X 1.3.

portion of the occipital condyle and enclose the foramen magnum. The exoccipitals articulate dorsally with the supraoccipital and the epiotics

and laterally with the intercalars. The median line of contact between the exoccipitals is marked by a prominent vertical ridge. Well-developed inter-

calars (Figs 4, 6) form the postero-ventral corners of the neurocranium. They join the lateral margins of the exoccipitals by an interdigitating suture and adjoin the postero-ventral corner of the pterotics. The subtemporal fossa is not evident.

The epiotics (Figs 4, 6) form the postero-dorsal corners of the neurocranium, lying dorsal to the exoccipitals and lateral to the supraoccipital. They combine with the pterotics to form the post-temporal fossa. This large fossa is roofed by the epiotics and appears to be oval, elongate dorso-ventrally with a central constriction at the suture between epiotic and pterotic.

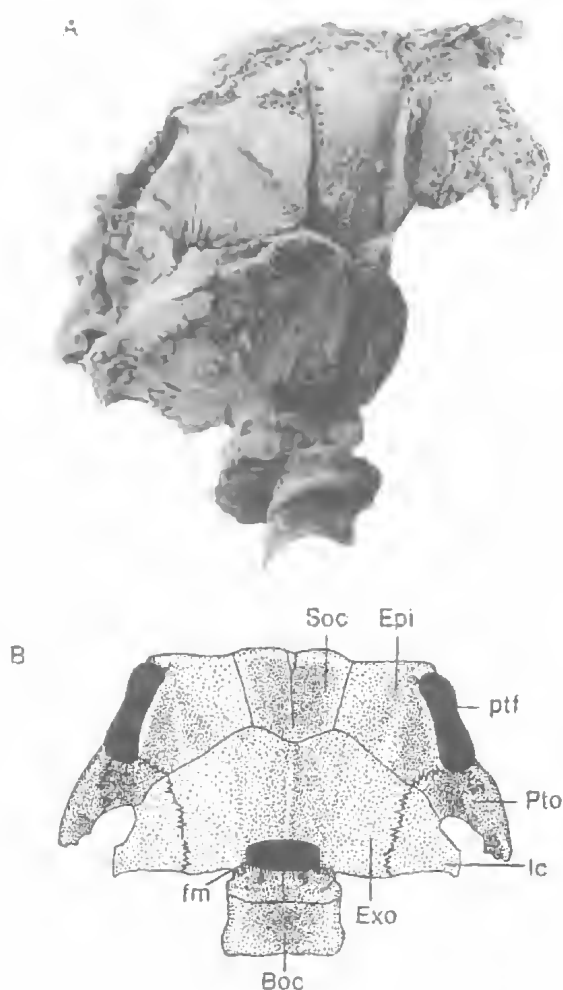


FIG. 6. *Dugaldia emmiltia* gen. et sp. nov. A. Holotype (GSQ 9242), Old, neurocranium, posterior view, X 4.1. B. Restoration of neurocranium in posterior view, X 2.1.

The supraoccipital (Figs 5, 6) lies medial to the epiotics and dorsal to the exoccipitals. Antero-dorsally it appears to join the parietals; however, this region of the skull is so badly weathered that it is impossible to ascertain the exact relationship between these two bones. Even so, the material preserved indicates that the supraoccipitals do not extend anteriorly to separate the parietals. The posterior face of the supraoccipital is markedly concave, with a small supraoccipital crest at the deepest point of the depression. When the neurocranium is viewed laterally the supraoccipital crest is not visible (Fig. 4).

The parasphenoid defines the ventral surface of the neurocranium. It is long, extending forwards from the posterior margin of the neurocranium to cover the dorsal surface of the vomer. The vomer is accommodated in the antero-ventral surface of the parasphenoid by means of a V-shaped depression. The remainder of the ventral surface of the parasphenoid is gently convex except beneath the otic region of the neurocranium. Here the (ventral) parasphenoid becomes gently concave and the lateral margins flare dorsally to form the ventral wall of the posterior myodome. The dorsal surface of the basisphenoid is sharply convex beneath the orbital region of the neurocranium and it then becomes concave beneath the otic region of the brain case forming the ventral compartment of the myodome. The parasphenoid is broadest anteriorly and posteriorly, constricting beneath the orbital section of the neurocranium. Longitudinally, the parasphenoid is gently convex ventrally beneath the orbital portion of the neurocranium. Behind its ascending process the parasphenoid is distinctly flexed through an angle of approximately 120 degrees. Its ascending process forms the postero-ventral margin of the orbital region of the brain case and shares an interdigitating suture with the prootic. At the base of the process a foramen for the internal carotid artery is evident. No teeth were found on the parasphenoid.

A basisphenoid (Fig. 4) extends from the alisphenoid (not visible) to the parasphenoid. It is a simple elongate shaft of bone with a flat lateral surface and a rounded ventral tip which articulates with the parasphenoid. The median vomer (Fig. 4) comprises a bulbous anterior head and a long tapering posterior process embedded in the parasphenoid. The antero-ventral surface of the head shows small hooked teeth on a tooth patch split by a mid-line groove. The antero-dorsal surface of the vomerine head is divided by a

mid-line groove which receives a projection from the dorsal ethmoid.

The ethmoid region of the neurocranium (Figs 4-5) is composed of four bones: the dorsal dermethmoid, the median mesethmoid and the paired lateral dermethmoid bones.

The dermethmoid (Figs 2, 4, 6) forms the anterior end of the dorsal surface of the neurocranium. It joins the frontals anteriorly by means of a semicircular denticulate suture. The anterior margin shows a medially situated anteriorly directed "nose", the ventral surface of which is embedded in the head of the vomer and overlies the dorsal surface of the mesethmoids.

The mesethmoid (Figs 4, 5) articulates with the vomer antero-ventrally, the dermethmoid postero-ventrally and the frontals postero-dorsally. Its anterior surface exhibits a slightly concave facet which doubtless received the articulating heads of the maxilla and premaxilla. A pair of lateral wings is situated on the mesethmoid slightly in advance of its antero-lateral junction with the frontal bones. These wings combine with the lateral dermethmoids to form the articular facet for the palatine bone.

The lateral dermethmoids (Figs 2, 4) lie postero-ventral to the mesethmoid and articulate with the frontals dorsally and the parasphenoid ventrally. The ventro-lateral half of the lateral dermethmoid, the ventral margin of which articulates with the parasphenoid, is basically square, with a large vertical indentation along its midline. The anterior margin of this portion of the lateral dermethmoid joins with the mesethmoid to form a facet for the palatine head. Postero-dorsally the dermethmoid contracts to form a strut which articulates by means of an expanded head with the ventral surface of the frontals.

HYOMANDIBULAR APPARATUS

The hyomandibular (Fig. 2) is composed of a large, dorsal head which contracts ventrally to join a strong ventrally directed shaft. The head, which is shaped like an irregular pentagon, is dominated medially by an extension of the ventral shaft. The dorsal margin of this polygon articulates with the hyomandibular fossa. Posteriorly the hyomandibular bone articulates with the opercular above and the preopercular below. There is no evidence that the hyomandibular has a preopercular process. Anteriorly the hyomandibular forms the rear margin of the orbit. Antero-ventrally it is covered by the metapterygoid.

The metapterygoid is sub-triangular in shape with a postero-ventrally directed apex. Its exterior

surface is gently concave, as is the dorsal margin. Antero-dorsally it articulates with the entopterygoid and ventrally it abuts the quadrate.

The quadrate is also sub-triangular in shape. Its blunt apex abuts the articular portion of the mandible. Posteriorly it is joined by the symplectic bone.

The symplectic is wedge-shaped with its base joining the ventral edge of the hyomandibular shaft. From here it extends ventrally to a point, wedging between the quadrate and the antero-ventral margin of the preopercular.

The entopterygoid joins the antero-dorsal corner of the quadrate. It is almost entirely concealed by the metapterygoid and the quadrate. Only the anterior dorsal surface is visible; this is gently concave and extends anteriorly to meet the palatine bone. The ectopterygoid is concealed.

The palatine is a short stout bone. Dorsally it is markedly concave. Anterodorsally it bears a concave head, shaped like a clover-leaf, which articulates with the facet formed by the ventral surface of the mesethmoid and the lateral dermethmoid. Antero-laterally the palatine head exhibits another concave facet which must have received the head of the maxilla.

HYOID ARCH, BRANCHIOSTEGALS AND GILL-ARCHES

The hyoid arch, branchiostegals and gill-arches (Fig. 4) are not well preserved. The posterior element of the ceratohyal is missing and none of the gill-arches has survived intact. The anterior ceratohyal is clearly visible. It is a strong, robust bone exhibiting a large oval 'berciform' foramen. A groove, for the efferent hyoidean artery, extends from the anterior margin of the foramen to the rounded antero-dorsal corner of the bone. The posterior margin of the anterior ceratohyal flexes anteriorly at an angle of approximately 120 degrees. The dorsal margin is slightly convex, and the ventral margin is gently sinuous. The ventral margin meets the posterior margin at an angle of approximately 45 degrees.

Both the dorsal and ventral hypohyals have been preserved, but are somewhat obscured by matrix and bone fragments. They are joined by means of a suture which is interdigitating anteriorly becoming simple posteriorly. At its mid-point this suture is dilated into a foramen. The lateral margins of these bones are difficult to discern, but it seems that they join together to produce a semicircular shape, curving anteriorly, with a slightly concave posterior margin.

Sixteen branchiostegal rays have been preserved, of which 11 meet the anterior ceratohyal. The other five presumably articulated with the missing posterior ceratohyal. Two types of branchiostegal ray are evident. Those adjoining the anterior ceratohyal are composed of a head which articulates with the ventral margin of the anterior ceratohyal. The head caps a cylindrical neck which expands into a posteriorly curved distal shaft. The lateral surface of the shaft exhibits a clearly defined, medially positioned, longitudinal groove which commences at the base of the cylindrical neck. The remaining branchiostegals are much simpler. The anterior, articulating portion of these rays is simply a short blunt projection from which the shaft expands distally to a broad, flat and gently curved ray.

Gill arches are not preserved. However, among the litter of bone fragments are abundant tooth plates, some bearing small, recurved teeth of uniform size. Evidently the apparatus was well toothed.

No gular plate is evident. It is not possible to determine if this is because it never existed or was not preserved.

DERMAL JAWS

Only the dentary (Fig. 2) has been preserved and this can be observed only from its exterior surface. It is short and deep, with a high coronoid process located approximately midway along the dorsal margin. Just behind the antero-dorsal edge of the dentary the dorsal margin flattens and curves medially into the short mandibular symphysis. In its anterior half the dorsal margin of the mandible bears small teeth of uniform size. On the lateral surface of the mandible, immediately below the anterior portion of the oral margin, is a deep V-shaped depression (apex directed anteriorly). The angulo-articular, triangular in shape, constitutes the postero-ventral portion of the mandible and forms the articular facet. A groove along the ventro-lateral margin of the dentary marks the path taken by the mandibular sensory canal.

CIRCUMORBITAL BONES

A single slender supraorbital and the incomplete remains of a sclerotic ring have been preserved (Fig. 2).

OPERCULAR BONES

(Fig. 2) The four bones of the opercular series (preopercular, opercular, subopercular and interopercular) have all been preserved. These thin

bones have all suffered some degree of damage along their margins.

The preopercular has a convex anterior margin which adjoins the hyomandibular, symplectic and quadrate. Posteriorly the preopercular meets the opercular, and ventrally it overlaps the interopercular. Sensory canals are indicated by ridges radiating from a point at approximately the mid-point of the anterior margin out to the posterior and ventral margins. The interopercular is mostly masked by the overlapping preopercular. It is oval in shape and the ventral quarter of the bone is curved medially.

The opercular has a rather badly damaged posterior margin. It appears to have been essentially semicircular in shape, with a convex posterior margin. The anterior margin shows a concave dorsal portion which articulates with the opercular process of the hyomandibular. The ventral two thirds of this margin are straight and join the preopercular ventrally. The opercular overlaps the subopercular and joins the cleithrum posteriorly. The subopercular is overlapped by the ventral margin of the opercular and the posterior portion of the interopercular. Consequently, something like a third of this bone is obscured from view. Like the interopercular it is curved medially. Most of the lateral surface of the subopercular is smooth and featureless, except where it abuts the anterior margin of the opercular bone. Here a narrow raised ridge is aligned parallel to the anterior margin of the opercular.

PECTORAL GIRDLE AND FINS

These bones are not well preserved and somewhat obscured by matrix and debris. The cleithrum is visible in lateral view, adjoining the posterior margins of both the opercular and subopercular bones. The anterior margin is gently curved both posteriorly and medially; the posterior margin bulges ventrally, giving the bone a 'd-shaped' appearance. The supracleithrum lies dorsal to the cleithrum, abutting the opercular bone, but is too poorly preserved to merit description. The post-temporal is not visible.

The partly-concealed scapular shows a fan-shaped dorsal head joined to a robust ventral stem which articulates with the coracoid. The coracoid, like the scapular, is only partly visible. The anterior portion is obscured from view and posteriorly it is only visible internally. A complex, posteriorly positioned head is evident articulating with the base of the scapular. From the head a long flat shaft of bone extends anteriorly, disappearing

beneath the posterior branchiostegal rays. Eleven pterygials are visible behind the coracoid head.

There are indications of 11 pectoral fin rays, and although these are poorly preserved they appear to have branched distally. The first three fin rays are distinctly broader than the rest.

VERTEBRAL COLUMN

Eighteen vertebrae are preserved. Their centra are deeper than long and marked laterally by three deep longitudinal grooves which give the vertebrae a ribbed appearance. It is not possible to determine whether or not the vertebrae are autogenous. The tail has not been preserved.

SQUAMATION

Some poorly preserved scales are visible. All appear to be identical and are large, thin and cycloid, showing concentric radii.

DISCUSSION

The many orders of neoteleosts have been distinguished on skeletal characters of the pharyngobranchial apparatus, upper jaw, rostrum and tail, along with characters of the soft tissues. Unfortunately the holotype of *Dugaldia emmilta* is not sufficiently well preserved to provide reliable information on these characters, so that it cannot be allocated to any particular order of neoteleosts.

A tripartite occipital condyle, comprising exoccipitals and basioccipital, has been regarded as a character defining the neoteleosts (Patterson, 1964; Rosen & Patterson, 1967; Fink & Weitzman, 1982; Lauder & Liem, 1983). Its occurrence in *Dugaldia emmilta* would seem to indicate affinities with this group. However, it should be noted that a tripartite occipital condyle has also been reported in some members of the Salmonidae (Fink & Weitzman, 1982; Lauder & Liem, 1983). On this basis Fink and Weitzman (1983) suggested that the Salmonidae should be regarded as the sister group of neoteleosts, a view which was adopted by Lauder and Liem (1983).

Rosen (1985) disagreed with this view, contending that the tripartite occipital condyle does not occur throughout the Salmonidae. He stated "... this type of joint has a limited distribution only in recent salmonines and is therefore probably convergent." His conclusion was supported by Cavender and Miller (1972) who reviewed the occipital joints of modern and fossil salmonids.

It is difficult to assess the salmonid affinities of *Dugaldia* because the Salmonidae might not be a monophyletic group (Fink & Weitzman, 1982;

Lauder & Liem, 1983; Rosen, 1985). Rosen (1974), in his study of salmoniform fishes, used both the form of the pharyngobranchial apparatus and the caudal skeleton to characterize salmoniforms. Unfortunately, the caudal skeleton has not been preserved in *Dugaldia emmilta* and the pharyngobranchial apparatus has been badly damaged. One feature on which Rosen placed particular emphasis was the arrangement of teeth on basihyal and basibranchial tooth plates. He considered that in their primitive arrangement these teeth "are small, uniform and close set. Among salmoniforms this basic pattern is modified in various ways" (Rosen 1974, p. 273). The incomplete basibranchial toothplate preserved in *Dugaldia* reveals a tooth pattern similar to the primitive pattern described by Rosen (1974). All the teeth appear to be small and uniform in size with the teeth on the margin of the plate showing no evidence of enlargement, which suggests that *Dugaldia* is not a salmonid.

However, more recent work (Fink & Weitzman, 1982) questioned the value of using the presence of a modified tooth pattern on the basihyal and basibranchial tooth plates to characterize salmonids. In contrast to Rosen (1974), Fink and Weitzman (1982) found some salmonids in which the teeth of the basihyal had not been modified from the small uniform tooth pattern described by Rosen (1974).

Overall, the skeletal evidence separating *Dugaldia emmilta* from the salmonids is equivocal. However, the modern natural distribution of the Salmonidae is confined to the Northern Hemisphere, and to date no salmonids have been recorded from the Early Cretaceous of the Southern Hemisphere. The family Galaxiidae does occur in Australia and has been grouped with the Salmonidae in the order Salmonoidei. However most workers (Fink & Weitzman, 1982; Lauder & Liem, 1983; Rosen, 1985) believe that the galaxiids should not be included in this group. *Dugaldia emmilta* shows little similarity with the galaxiids which lack a tripartite occipital condyle. Consequently it seems unlikely that *Dugaldia emmilta* is a member of the Salmonidae and that it is better placed with the neoteleosts.

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ABBREVIATIONS

Boc-basioccipital; Bsp-basisphenoid; Brr-bran-
chiostegal rays; Cer-ceratohyal; Cl-cleithrum;
De-dermethmoid; Den-dentary; Enp- endoptery-
goid; Epi-epiotic; Exo-exoccipital; fm-foramen
magnum; Fm-formation; Fr-frontal; GSQ-Geo-
logical Survey of Queensland; Hm-hyoman-
dibular; Ic-intercalar; Iop-interopercular;
Lde-lateral dermethmoid; Lhp-lower hypohyal;
Mes-mesethmoid; Mpt-metapterygoid; Op-oper-
culum; Pa-parietal; Pal-palatine; Pop-preoper-
culum; Pro-prootic; Psp-prasphenoid; ptf-post-
temporal fossa; Pto-pterotic; Qld-Queensland;
Qu-quadrate; Sclr-sclerotic; Spo-sphenotic;
So-supraorbital; Soc-supraoccipital; Sop-sub-
opercular; Sy-sym- plectic; Uhp-upper hypohyal;
Vo-vomer.

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